The Head Shield of *Tiaraspis subtilis* (Gross) [Pisces, Arthrodira]

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The head shield of *Tiaraspis subtilis* (Gross, 1933) is described. Very large orbits, large preorbital plates possibly including the postnasals, a 'fontanel' between pineal and rostral plates, and a club-shaped nuchal plate, in addition to the previously known high pointed median dorsal plate, are distinctive features of *Tiaraspis*. *Tiaraspis* is a phlyctaeniine arthrodire whose head shield resembles that of Groenlandaspididae. This resemblance supports their close relationship as suggested by Ritchie (1974, 1975) based on the trunk shield alone. This close relationship between these two genera is made tenable if the Holonematidae are not considered to be close relatives of the Groenlandaspididae.

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INTRODUCTION

Gross (1962) founded the new genus *Tiaraspis* on trunk shield parts which he described earlier (Gross, 1933a, 1937). He reconstructed the whole trunk shield with the characteristic high and narrow median dorsal plate. This median dorsal plate is easily recognized and the genus was discovered in other localities soon thereafter (Gross, 1965; Schmidt and Ziegler, 1965; and in Odenspiel, an as yet unpublished Early Devonian locality in the eastern Rheinisches Schiefergebirge). All these localities furnished only isolated parts of the trunk shield, and the head shield remained unknown until 1977 when the author together with Mr P. Brühn, Essen, West Germany, began a specific search for the head shield at the Siesel locality, east of Plettenberg, eastern Rheinisches Schiefergebirge (see Schmidt and Ziegler, 1965).

In the meantime, Ritchie (1974, 1975) allied the Early Devonian *Tiaraspis* with *Groenlandaspis* from the Middle and Late Devonian, based on features of the trunk shield. He postulated an unusual evolution from a short trunk shield with a high median dorsal plate in *Tiaraspis,* to a long trunk shield with a low median dorsal plate in *Groenlandaspis*. The new material of *Tiaraspis* described here enables Ritchie's hypothesis based on the trunk shield to be checked with data from the head shield.

MATERIALS AND METHODS

During 1977, Mr P. Brühn, Essen, and the author collected at different times in the dark-grey shales of the Lower Devonian Rimmert Formation at Siesel, east of Plettenberg, eastern Rheinisch Schiefergebirge. Remains of *Tiaraspis* are very common at this locality; only three acanthodian spines (Fig. 5**B, C**) have been discovered besides remains of *Tiaraspis*. The latter include three head shields and one isolated central plate, all in close association with trunk shield parts.

The shales of the Rimmert Formation at Siesel show cleavage oblique to the bedding, and the specimens are partly deformed. I have therefore desisted from reporting measurements. The head shield was reconstructed from the least deformed specimen (Gö 807-1). A plasticine model was built after the head shield and the trunk

shield as reconstructed by Gross (1962). The author's reconstruction of *Tiaraspis* (Fig. 3) was drawn from the plasticine model.

The material is deposited in the Geologisch-Paläontologisches Institut and Museum, Universität Göttingen, West Germany (Gö 807-1 to 7), and in the private collection of Mr P. Brühn, Essen (Br. 0208).

Systematics

Class PLACODERMI M'Coy, 1848
Order ARTHRODIRA Wodoward, 1891
Suborder PHLYCTAENIINA Denison, 1978
Family GROENLANDASPIDIDAE Obruchev, 1964
Genus *TIARASPIS* Gross, 1962
Tiaraspis subtilis (Gross, 1933)
Figs. 1-4, 5**A**

1929. *Didymaspis*(?) Steinmann and Elberskirch, p.10.
1933a. *Acanthaspis subtilis* n.sp. Gross, pp. 61-62, fig. 9. 2-13; pl. 4, figs. 3, 4, 8.
1933a. *incertae sedis* (freie stachelartige Platte) Gross, p. 69, fig. 14; pl. 5, fig. 8.
1933b. *Acanthaspis subtilis* Gross. Gross, p. 24.
1933. *Acanthaspis subtilis* Gross. Schriel, p. 12.
1937. *Prosphymaspis* n.gen. *subtilis* (Gross). Gross, p. 24, fig. 12D-F.
1937. Arthrodire *incertae sedis.* Gross, p. 43, fig. 14A-C; pl. 3, fig. 1.
1962. *Tiaraspis* n.gen. *subtilis* (Gross 1933). Gross, pp. 46-56, figs. 1-7A.
1965. *Tiaraspis subtilis* (W. Gross). Gross, pp. 15, 16.
1965. *Tiaraspis subtilis* (Gross). Schmidt and Ziegler, p. 226, fig. 1.
1969. *Tiaraspis subtilis* (Gross). Miles, p. 147.
1974. *Tiaraspis.* Ritchie, pp. 34, 35.
1975. *Tiaraspis subtilis* (Gross). Ritchie, p. 570, fig. 1.
1978. *T. subtilis* (Gross) 1933c. Denison, p. 65, fig. 44D.

Diagnosis: Phlyctaeniid arthrodire with a very high pointed median dorsal plate. Anterior and posterior dorso-lateral plates deep and short, curving first inward above the lateral line canal, then dorsally to be overlapped by the median dorsal. The lateral line curves strongly dorsad on the posterior dorsolateral plate. Low and small pectoral fenestra bordered posteriorly by long posterior lateral and posterior ventrolateral plates. Long, medially-barbed spinal plates. Posterior ventrolateral plates end in sharp points with a deep median embayment, the right posterior ventrolateral plate overlapping the left one anteriorly and overlapped by the left one posteriorly.

Head shield with straight posterior border and large orbits. Club-shaped nuchal plate broader anteriorly than posteriorly, with embayment posteriorly for the paranuchal plate. Small postmarginal, marginal and postorbital plates. Long preorbital plates placed laterally to a small pineal plate, a broad rostral plate, and a median space not covered by bone between the pineal and rostral. Supraorbital sensory line canal and central sensory line canal entering the central plate, postmarginal sensory canal entering the postmarginal plate, occipital cross commissure forming a canal on the paranuchal plate towards the posterior end of the nuchal/paranuchal suture, and posterior pitline running parallel to the endolymphatic duct from the growth centre of the paranuchal plate towards the point of junction formed by nuchal, central and paranuchal plates.

Holotype: Anterior ventrolateral plate (Gross, 1933a: pl. 4, fig. 8; Gross, 1962: fig. 3F), Humboldt Museum für Naturkunde, Berlin, Germany.

Type locality and horizon: Quarry Heider at Overath, southeast of Köln, eastern Rheinisches Schiefergebirge, West Germany, in Wahnbach Formation (? Late Siegenian, Early Devonian).

New material: Specimens Gö 807-1 (Figs 1**B**, 5**A**) Gö 807-2 (Figs 1**A**, 4**A**), Gö 807-3 (Figs 1**C**, 4**B**), and Gö 807-4 (an isolated central plate) from Siesel, east of Plettenberg, eastern Rheinisches Schiefergebirge, in the Rimmert Formation (? Early Emsian, Early Devonian).

Specimen Br. 0208, a skull from Odenspiel, southeast of Gummersbach, eastern Rheinisches Schiefergebirge, in the Odenspiel Formation (? Late Siegenian, Early Devonian).

Description: The posterior and central parts of the head shield are preserved in all four skull specimens. The central and paranuchal plates occupy most of the postpineal part of the skull. The paranuchal plates fill wide posterior embayments in the lateral margins of the nuchal plate, making the latter club-shaped with a three-lobed anterior portion which is twice as wide as the posterior portion. The nuchal and paranuchal plates form a straight posterior margin to the head shield. The paranuchal plate extends forward nearly half the length of the central plate and is bordered anterolaterally by the small postmarginal and marginal plates. The postmarginal (not shown in Fig. 1**B**) is represented in the counterpart, Gö 807-1b. The central plates are irregular in shape with a posterior extension between nuchal and paranuchal plates. Laterally, the central plate is bordered by marginal and postorbital plates, and by the preorbital plate anteriorly. The posterior part of the pineal plate lies between the central plates, with the anterior part between the posterior part of the preorbitals. The pineal plate is small, and is broken horizontally so that the pineal pit appears as an opening in specimen Gö 807-1a. The pineal plate does not reach the rostral plate and there is an empty space or 'fontanel' between these bones. The rostral plate forms the undulating anterior border of the head shield, and lies between the anterior part of the long preorbitals. The preorbitals may include the postnasal plates in their anterior portion; they form the dorsal and anterior borders of the large orbit, while the postorbitals occupy only a short part of the posterior margin of the orbits. The sclerotic plates are preserved in specimen Gö 807-1, and are partly superimposed on each other; I count four of them, the typical number for arthrodires (Denison, 1978).

The sensory line canals follow the usual course for phlyctaeniid arthrodires, except that the supraorbital sensory canal passes onto the central plate. The occipital cross commissure and the posterior pit line form canals on the paranuchal plate. The occipital cross commissure canal leaves the paranuchal mediad close to the posterior narrow portion of the nuchal. This could indicate the presence of a short unpaired extrascapular plate behind the nuchal plate. The middle pit line and the anterior part of the posterior pit line form distinct grooves on the central plates. The posterior part of the posterior pit line runs in a canal from the growth centre of the paranuchal plate anteriorly towards the junction formed by the nuchal, paranuchal and central plates. The endolymphatic duct presumably opened externally near the growth centre of the paranuchal, as is normal in phlyctaeniids. The canal for the duct can be seen running anteriorly within the bone beneath the posterior pitline, but its posterior end is not clear.

Reconstruction: The reconstruction (Fig. 3) of *Tiaraspis subtilis* is based on the reconstructed head shield (Fig. 2), and the trunk shield as reconstructed by Gross (1962: fig. 6). The size of the latter has been adjusted to conform to the head shield by comparison with the trunk shield parts associated with the head shields. The plasticine model shows

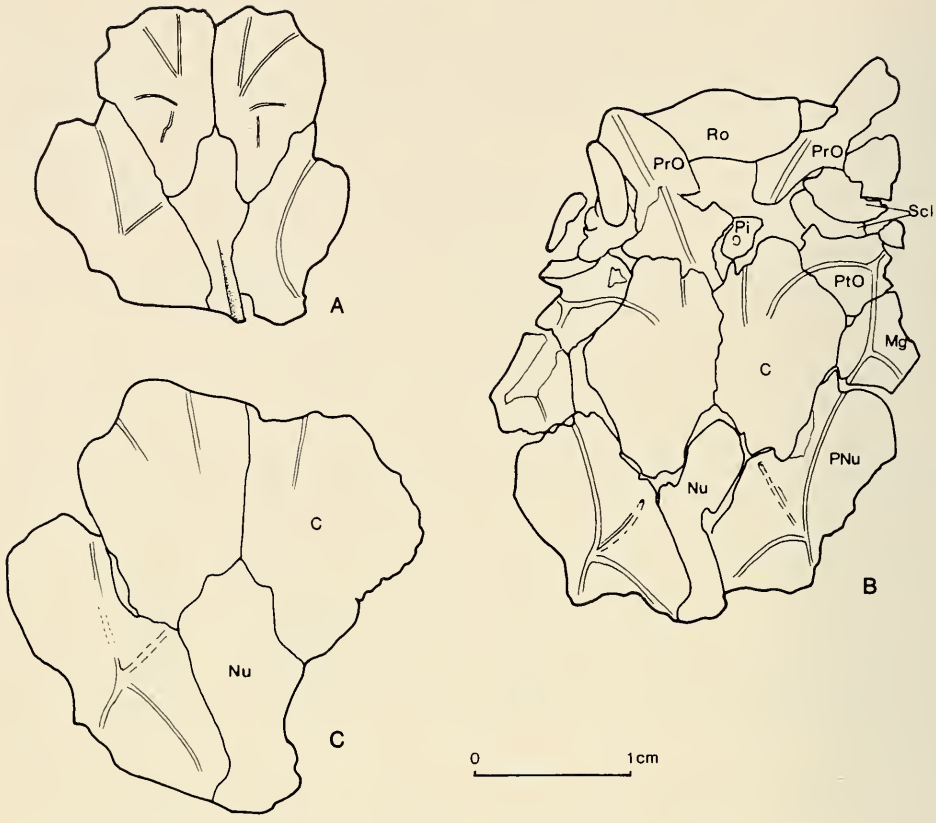


Fig. 1. Head shields of *Tiaraspis subtilis* (Gross) from the Early Devonian of Siesel, West Germany. **A**, Gö 807-2; **B**, Gö 807-1a; **C**, Gö 807-3. *C*, central plate; *Mg*, marginal plate; *Nu*, nuchal plate; *Pi*, pineal plate; *PNu*, paranuchal plate; *PrO*, preorbital plate; *Pto*, postorbital plate; *Ro*, rostral plate; *Scl*, sclerotic plate.

that the trunk shield is lower in lateral view than drawn by Gross (1962: fig. 6B) because the ventral portion of the antero-lateral plate turns horizontally so that the plate shortens dorsoventrally in lateral view. The head shield is long in comparison to the dorsal trunk shield (head shield 1.5 times the length of the trunk shield at lateral line canal level), and in comparison to relative length in other phlyctaeniines, especially holonematids. Even *Groenlandaspis* has a proportionately longer trunk shield.

The greatest difference from other phlyctaeniines can be found in the lateral side of the head. As restored, the large orbits leave little space for the suborbitals (not known), and this bone was presumably high and short. The submarginal is assumed to have occupied the normal position below the postorbital, marginal and postmarginal plates. The large orbits give *Tiaraspis* some resemblance to advanced brachythoracid arthrodires from the Late Devonian, some of which also possess 'fontanels' on the head shield, but in a more posterior position.

Geological age: The genus *Tiaraspis* is restricted to the Early Devonian (Gross, 1965). The assignment of the median dorsal plate of *Tiaraspis* sp. indet. to the Late Devonian of Modave, Belgium, was questioned by Gross (1965). At present, the genus is restricted geographically to central Europe. It is questionable that the median dorsal

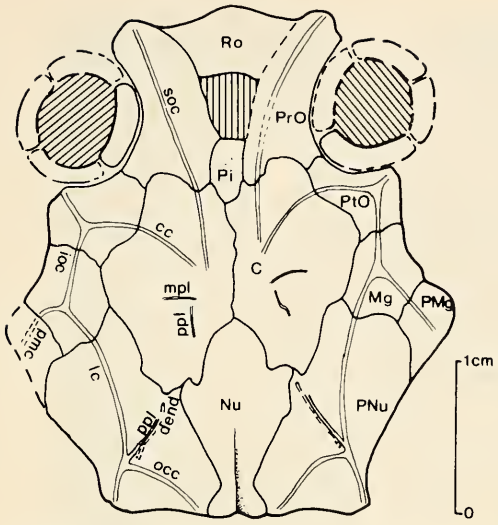


Fig. 2. Reconstruction of the head shield of *Tiaraspis subtilis* (Gross), mainly after Gö 807-1.
C, central plate; *cc,* central sensory line canal; *dend,* endolymphatic duct; *ioc,* infraorbital sensory line canal; *lc,* main line canal; *Mg,* marginal plate; *mpl,* middle pit line groove; *Nu,* nuchal plate; *occ,* occipital cross commissure canal; *Pi,* pineal plate; *pmc,* postmarginal sensory line canal; *PMg,* postmarginal plate; *PNu,* paranuchal plate; *ppl,* posterior pit line groove; *PrO,* preorbital plate; *PtO,* postorbital plate; *Ro,* rostral plate; *soc,* supraorbital sensory line canal.

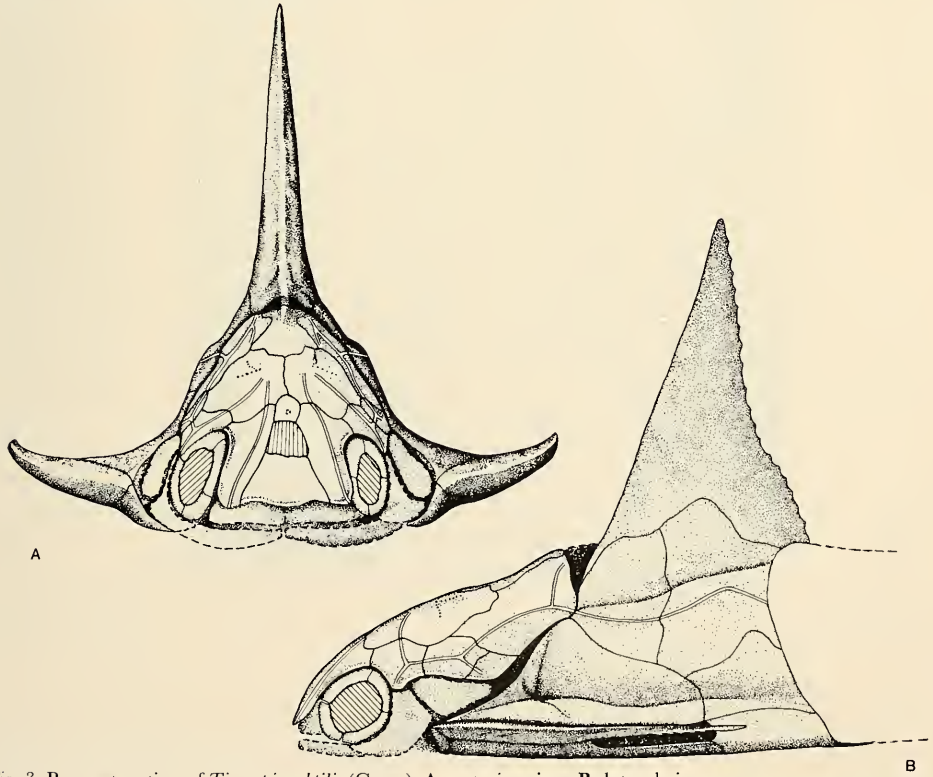


Fig. 3. Reconstruction of *Tiaraspis subtilis* (Gross). **A**, anterior view; **B**, lateral view.

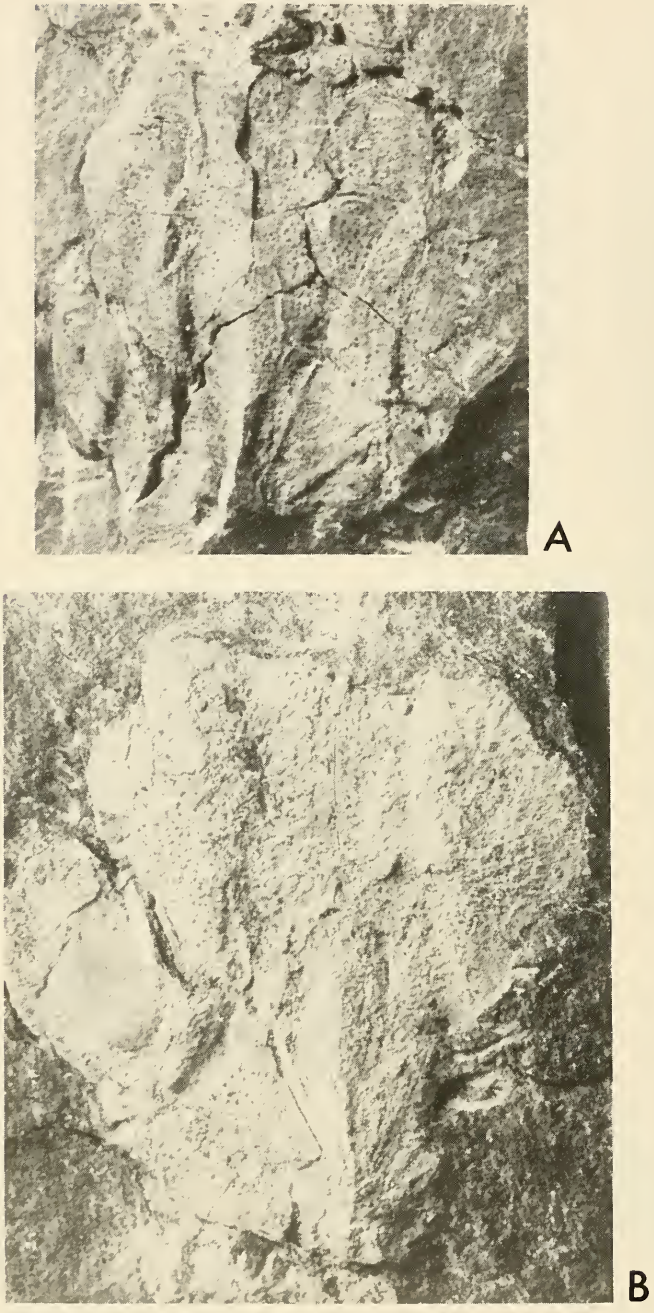


Fig. 4. Tiaraspis subtilis (Gross) from the Early Devonian of Siesel, West Germany. **A**, specimen Gö 807-2 (× 2); **B**, Specimen Gö 807-3 (× 2).

plate described by Gross (1965) from the Early Devonian of Spitsbergen belongs to this genus.

The species *Tiaraspis subtilis* occurs only in rocks of late Early Devonian age. The as yet undescribed fauna from Odenspiel is similar to that of Overath (Gross, 1933a, b, 1937, 1962). Both the Odenspiel Formation and the Wahnbach Formation of Overath are considered to be Late Siegenian (graben and Hilden, 1972; Schriel, 1933). the identification of the Siegenian index fossil *Rhenorensselaeria crassicosta* from Overath was questioned by Jux (1964). He considers the Wahnbach Formation as part of the Bensberg Formation, and the latter as Early Emsian in age. Jux (1982) correlates the Wahnbach Formation of Overath with the Odenspiel Formation, and assigns them a Late Siegenian and/or Early Emsian age. The Rimmert Formation, at least in its lower part, is of Early Emsian age according to Schmidt and Ziegler (1965), based on the occurrence of *T. subtilis*. Besides *T. subtilis, Gyracanthus? convexus* Gross 1933 occurs at Overath and at Siesel (Fig. 5**B**), and this supports the conclusion of Schmidt and Ziegler (1965). *T. subtilis* has been recorded from another Early Emsian locality in the western Rheinisches Schiefergebirge (Kahlenberg, east of Neroth; Gross, 1933b: 24), and also from the Lower Siegenian (Schmidt and Ziegler, 1965: 226). To summarize, *T. subtilis* is apparently restricted to the Siegenian and Early Emsian in the Early Devonian, but is most common in Late Siegenian/Early Emsian strata.

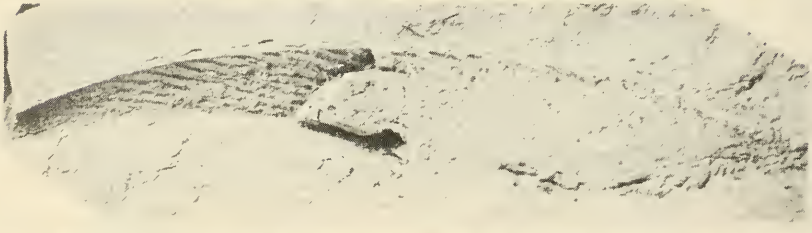
Relationships

The trunk shield of *Tiaraspis* is quite characteristic. The median dorsal plate alone makes the genus easily distinguishable from all other known arthrodires, and Miles (1969) placed it in its own family, the Tiaraspididae. Earlier, Gross (1962) noted similarities in the median dorsal plate with some antiarchs, Ptyctodontida, Arthrodira incertae sedis *(Grazosteus),* and those of *Huginaspis* and *Prosphymaspis*. Ritchie (1974, 1975) placed *Tiaraspis* with *Groenlandaspis* in the family Groenlandaspididae Obruchev, 1964, which is characterized by many primitive and some advanced features. A long, narrow median dorsal plate, no paired antero-ventral plates, an angular, dorsally directed flexure of the lateral line canal on the posterior dorsolateral plate, and a well-developed craniothoracic articulation are also characteristic of the Holonematidae. Therefore Denison (1978) united the Tiaraspididae and Groenlandaspididae with the Holonematidae, thereby following Obruchev's (1964) proposal that the latter two families be grouped together. The short, deep anterior dorsolateral and posterior dorsolateral plates distinguish *Tiaraspis* and *Groenlandaspis* from members of the family Holonematidae *sensu stricto*. Young (1981) accepted the close relationship of *Tiaraspis* with *Groenlandaspis* and *Holonema* (Fig. 6**A**), but on the other hand Dennis and Miles (1979a, b, 1980, 1982) regarded *Holonema* as a primitive brachythoracid (see also Miles, 1973).

That the Phlyctaeniidae and Holonematidae (+ Groenlandaspididae and Tiaraspididae) are closely related to each other is supported by the long trunk shield, long and narrow median dorsal plate, and the loss of anterior ventral plates as shared derived characters. A differentiated exoskeletal articulation connects the head shield with the trunk shield. *Tiaraspis* clearly belongs within Denison's (1978) suborder Phlyctaeniina, even though it may not possess a ventral ridge on the median dorsal plate, and the two pairs of superognathals are not yet known.

It is difficult to find advanced characters which separate the families within the Phlyctaeniina, as is always the case in primitive groups. The straight posterior border of the head shield is characteristic of Phlyctaeniidae, nevertheless Young and Gorter (1981) place *Denisonosteus,* a genus with a distinctly convex posterior margin, within the

A



B

C

Phlyctaeniidae. However *Tiaraspis,* with a nuchal plate similar to *Denisonosteus,* has a straight posterior margin, and no postnuchal process of the paranuchal plate as in phlyctaeniids, and is herein distinctly different from *Groenlandaspis.* Also, rostral and postnasal plates fused with each other may be an advanced character of the Holonematidae, but on the evidence of *Tiaraspis* this does not apply to the Groenlandaspididae (contrary to Young, 1981: fig. 17). Judging from the course of the supraorbital sensory canal, the postnasal in *Tiaraspis* and in *Groenlandaspis* seems to be fused with the preorbitals rather than with the rostral, unless it is a separate element lost from the skull in the available specimens. *Tiaraspis* also has a small pineal plate in the same position as the posterior part of the pineal plate in *Groenlandaspis.*

The lack of the advanced nuchal features and the straight posterior margin of the head shield exclude *Tiaraspis* from the Holonematidae in the sense of Denison (1978; *Holonema* up to *Groenlandaspis,* Fig. 6**A**). In contrast, the preorbital plate probably fused with the postnasal, the high pointed, laterally compressed median dorsal plate, and the high and short anterior and posterior dorsolateral plates unite *Tiaraspis* with *Groenlandaspis* (Fig. 6**B**). The Holonematidae are characterized by a very long trunk shield with a long, but not dorsally-pointed median dorsal plate, long anterior and posterior dorsolateral plates, long anterior lateral plate, and a very long, laterally directed pectoral fenestra. They are quite distinct from the Phlyctaeniina in these trunk shield characters and in features of the head shield (large rostro-postnasal plate, relatively small preorbital and central plates, deep cheek region with large suborbital plate). Therefore, I prefer to follow Dennis and Miles (1979a, b, 1980) and Ritchie (1975), and exclude the Holonematidae from the Phlyctaeniina; the discussion of their relationships is outside the scope of this paper. Still, the above arrangement does not eliminate the independent acquisition (Young, 1981: 269) of some characters (labelled 4 and 3c in Fig. 6**B**) within the Groenlandaspididae, and brachythoracid arthrodires including the Holonematidae. A detailed study of better-preserved skull shield material of Groenlandaspididae may reveal that these features indicate only superficial similarity. Another such independent acquisition would have to be postulated for the rostro-postnasal plate in *Arctolepis* and *Holonema.* The rostro-postnasal plate has in both forms quite a different relation to bordering plates and to the supraorbital sensory canal. In conclusion, *Tiaraspis* can be placed within the Groenlandaspididae by excluding the Holonematidae from the Phlyctaeniina. The family definition by Ritchie (1975) must be changed slightly regarding the head shield: head shield with straight or convex posterior margin, preorbital probably fused with postnasal, supraorbital sensory canal extending on to the central plate, large pineal plate or pineal plate + 'fontanel' between preorbital plates. *Tiaraspis* is more primitive in cranial features (4a-c in Fig. 6**B**) than *Groenlandaspis.* A convex posterior margin of the head shield may not be a distinctive character because it occurs also in *Denisonosteus,* an otherwise undoubted phlyctaeniid.

Finally the very high median dorsal plate and the large orbits of *Tiaraspis* could be associated with small body size; but this seems unlikely since *Groenlandaspis* with a much lower median dorsal plate is not much larger than *Tiaraspis.* Large orbits are typical for small fishes, but this is not so in arthrodires; small orbits occur not only in large, but also in small phlyctaeniines. Therefore the very high median dorsal plate and the

Fig. 5. **A**, head shield of *Tiaraspis subtilis* (Gross) from the Early Devonian of Siesel, West Germany. Specimen Gö 807-1a (× 2). **B**, **C**, acanthodian spines from the same locality. **B**, *Gyracanthus? convexus* Gross 1933. Specimen Gö 807-5, coated with ammonium chloride (× 3); **C**, climatiid acanthodian, Gö 807-6, a left pectoral spine in ventral view (× 4).

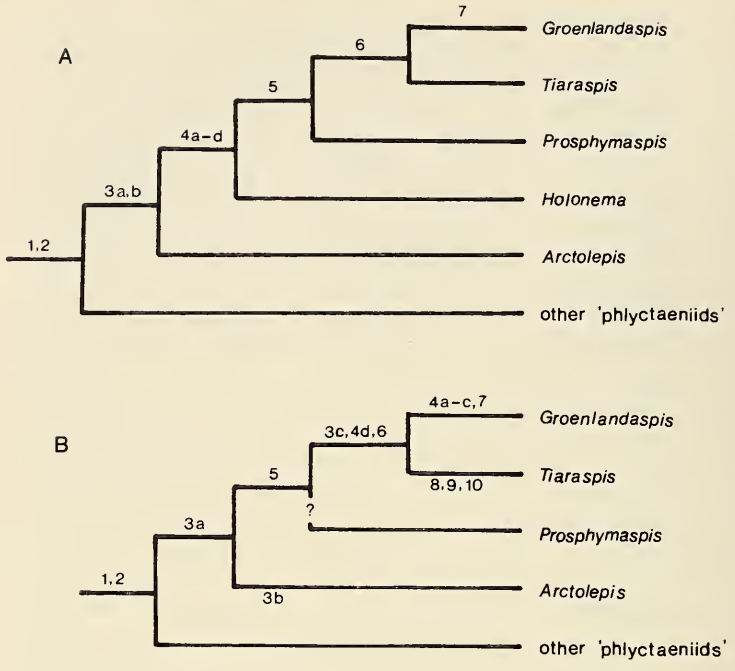


Fig. 6. **A**, Relationship scheme of Phlyctaeniina after Young (1981: fig. 16B). **B**, Here favoured relationship scheme of Phlyctaeniina without *Holonema*. Characters:
1, median dorsal plate long and narrow; 2, elongation of spinal plate; 3a, large pineal plate between preorbital plates, 3b, wide rostral plate which may incorporate fused postnasal, 3c, long preorbital plate which may incorporate postnasal; 4a, head shield with convex, angular posterior margin, 4b, paranuchal plate with postnuchal process, 4c, nuchal thickening, 4d, supraorbital sensory canal extending on to central plate; 5, high anterior and posterior dorsolateral plates, dorsally pointed median dorsal plate; 6, dorsal flexure of lateral line canal on posterior dorsolateral plate; 7, dorsal symphysis between posterior dorsolateral plates; 8, club-shaped, trilobate nuchal plate; 9, small pineal plate between preorbital plates with 'fontanel' in front; 10, large orbits.

large orbits are autapomorphies of *Tiaraspis* which may not be a common feature of the common ancestor of *Tiaraspis* and *Groenlandaspis*.

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This paper is dedicated to the late Prof. Dr W. Gross and to Dr A. Ritchie, Sydney, the two prominent students of the genus.

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